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Demography and Reproductive Biology of the Gopher Tortoise (*Gopherus Polyphemus*) Population at White Oak Plantation, Nassau County, Florida

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DEMOGRAPHY AND REPRODUCTIVE BIOLOGY OF THE GOPHER TORTOISE
(*GOPHERUS POLYPHEMUS*) POPULATION AT WHITE OAK PLANTATION, NASSAU
COUNTY, FLORIDA

by

Julia Rachel Smith

A thesis submitted to the Department of Biology in partial fulfillment of the
requirements for the degree of

Master of Science in Biology

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COLLEGE OF ARTS AND SCIENCES

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CERTIFICATE OF APPROVAL

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DEDICATION

I would like to dedicate this thesis to none other than the gopher tortoises. Not only could I not have done this project without them, but also they are truly one of the more marvelous creatures on this planet. Aside from conducting demographic research, I had the opportunity to learn of each tortoise's individuality and specialness, an experience I will never forget. So, tortoises, this one is for you.

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ABSTRACT

The demography and reproductive biology of the gopher tortoise (*Gopherus polyphemus*) was studied for two years at White Oak Plantation (WOP), located in northeast Florida along the St. Mary's river. Two sub-populations were studied in regions I referred to as Site A and Site B. I located 312 burrows and captured 109 different tortoises, either by hand or using bucket traps. Tortoise density was 4.48/ha at Site A and only 1.15/ha at Site B. Juveniles were the most abundant age class overall, while hatchlings were numerous at Site A but virtually absent at Site B. The combined sex ratio for adult tortoises at WOP was 1:1.55 (F:M). Six nests were discovered over the course of the study, all located at Site A. Mean clutch size was 3.8, much lower than other studies conducted in Florida and Georgia, but egg hatching success (87.5%) was comparable to other studies. Growth rates were mostly consistent with other studies for juvenile, sub-adult and adult age classes, but were unusually high for hatchlings. In light of the fact that habitat fragmentation is currently one of the leading threats to tortoise populations, I propose management recommendations that will merge these two sub-populations and lead to increased potential and gene flow for their long-term viability.

KEY WORDS: demography, Florida, gopher tortoise, *Gopherus polyphemus*, growth, reproduction, White Oak Plantation

INTRODUCTION

Life History of the Gopher Tortoise

The gopher tortoise (*Gopherus polyphemus*) is a medium-sized land turtle distributed throughout the southeastern coastal plain of the United States (Ernst and Lovich, 2009). It constructs burrows used for refuge that on average extend 4.5 m in length and 2.0 m in depth, and thus it requires sandy soils for efficient burrow excavation (Diemer, 1989; Mushinsky et al., 2006). The gopher tortoise primarily inhabits longleaf pine (*Pinus palustris*) forests and other sandhill habitats from Louisiana east to Florida, and north to South Carolina (Auffenberg and Franz, 1982; Diemer, 1986). In the southeastern coastal plain, the distribution of gopher tortoises is most correlated with the distribution of longleaf pine forests (U.S. Fish and Wildlife Service, 1990). Longleaf pine forest offers ideal habitat for the gopher tortoise because they have well-drained soils (which lower the risk of burrow flooding), open canopy (direct sunlight to the forest floor) which facilitates tortoise thermoregulation (Mushinsky et al., 2006), and abundant herbaceous groundcover (wiregrass and other groundstory plants) that provides the high forage quality preferred by gopher tortoises (Macdonald and Mushinsky, 1988).

The gopher tortoise is considered to be both a keystone species and an ecosystem engineer in the longleaf pine/sandhill community (Eisenberg, 1983; Diemer, 1986) because it disperses seeds for native grasses and other groundstory plants, and digs deep underground burrows that provide refuge for over 300 other

native species (Diemer, 1986; Jackson and Milstrey, 1989). Burrow commensal animals include the declining eastern diamondback rattlesnake (*Crotalus adamanteus*), Florida pine snake (*Pituophis melanoleucas mugitus*) and also protected species such as the indigo snake (*Drymarchon corais couperi*) and the Florida gopher frog (*Rana capito*) (Diemer, 1986; Kent et al., 1997).

Conservation Status

The U.S. Fish and Wildlife Service (USFWS) listed the gopher tortoise as “threatened” in its western range (which includes Louisiana, Mississippi and Alabama west of the Mobile and Tombigbee rivers) in 1987 (Wilson et al., 1997). The USFWS’s 12-month finding to list the gopher tortoise as “threatened” in its eastern range (encompassing South Carolina, Georgia, Florida and Alabama east of the Mobile and Tombigbee rivers) stated that the petition warranted federal protection for the tortoise, but higher priority listing actions require that it be placed on the list of candidate species for federal listing (USFWS, 2011). The gopher tortoise is currently listed as “threatened” by the state of Florida and it has some form of state protection in five of the six states encompassing its range. Louisiana gopher tortoises do not have state listing, but are still protected federally (Mushinsky et al., 2006).

Decline in Gopher Tortoise Populations

It is estimated that gopher tortoise numbers have declined by over 80% in the last 120 years (Auffenburg and Franz, 1982). Habitat destruction, degradation and fragmentation are cited as the main causes for the decline in gopher tortoise populations (Auffenburg and Franz, 1982; Lohofener and Loemeier, 1984). In Florida, only three percent of longleaf pine stands first documented 200 years ago remain (Kautz, 1993). These forests have gradually disappeared due to commercial development and replacement with different pine species that are more suitable for planted pine plantations, most often slash pine (*P. elliotii*) and loblolly pine (*P. taeda*).

Much of the longleaf pine forest has also been lost to urban development and agricultural practices, as its loose sandy soil is a highly desirable substrate for the aforementioned human activities (Mushinsky et al., 2006). Development, whether for urban, agricultural or mining purposes, results in direct habitat loss, habitat degradation, and habitat fragmentation, all of which have detrimental effects on gopher tortoise populations.

The increased fragmentation of the longleaf pine forest has resulted in a reduction of the natural incidence of forest fires in these areas, which in turn is associated with decreased habitat quality due to reduced abundance of groundstory plants. A temporary solution to this problem has been to conduct periodic prescribed burns in longleaf pine forests inhabited by gopher tortoises. Tortoises

respond favorably to consistent fire maintenance as their herbaceous food sources become more abundant (Landers and Speake, 1980; Landers and Buckner, 1981).

Unlike the longleaf pine, the introduced slash, loblolly and sand pine (*Pinus clausa*) are fire-resistant and do not burn as efficiently during natural or controlled fires. Therefore, in areas where these species have been planted, groundstory plants (the primary food source of the gopher tortoise) receive less direct sunlight and grow poorly (Komarek, 1974). This effect has resulted in low tortoise density in areas predominated by slash pine (Thomas, 1978; Lohoefer and Loemeier, 1981; Diemer, 1986; Aresco and Guyer, 1999b). Landers and Buckner (1981) further state that sand pines should not be planted on former sandhill/longleaf habitat. Like slash pine, sand pine grows very densely, and the resulting canopy layer reduces the amount of sunlight reaching groundstory plants.

In the Conecuh National Forest of Alabama, Aresco and Guyer (1999a) found decreased growth rates and delayed sexual maturity in gopher tortoises inhabiting slash pine forests compared to those inhabiting longleaf pine forests. Again, this result appears to be due to reduced available forage for gopher tortoises caused by the absence of a periodic fire regime. The increase of slash pine plantations and forests is occurring simultaneously with the greater than 90% decline of longleaf pine stands throughout Florida (Rostal and Jones, 2002) which has resulted in the associated population decline of the gopher tortoise.

A final factor leading to the reduced number of gopher tortoises is also associated with habitat loss. A gopher tortoise will extend its home range or even

abandon degraded habitat altogether in search of more suitable habitat (Aresco and Guyer, 1999b) or reproductive females that have dispersed to higher quality habitats. Dispersal increases the likelihood that tortoises will cross major roads and highways, and Landers and Buckner (1981) reported vehicular traffic to be the foremost cause of gopher tortoise mortality at their study site in southern Georgia.

Significance of Study

The conservation of the gopher tortoise is of paramount importance because of this species' role as a designated keystone species and ecosystem engineer in upland habitats. In order to prevent further decline of the gopher tortoise, appropriate management plans must be developed that confront the multitude of anthropogenic activities threatening the gopher tortoise, such as urban development and habitat degradation by fire suppression. Management plans will be most effective when they reflect a comprehensive understanding of gopher tortoise life history information.

Throughout the gopher tortoise's range, numerous studies have assessed the demography and life history of this species on public land (Alford, 1980; Landers et al., 1982; Wright, 1982; Mushinsky et al., 1994; Diemer, 1986; Smith et al., 1997). Few studies, however, have examined the life history of gopher tortoises on private land because of the difficulty in gaining access to these areas (Hermann et al., 2002). In Florida, there are currently 2,378,338 ha of potential gopher tortoise habitat

located on private land, while there are only 753,272 ha on public land (Hector and Beyeler, 2010). Given the extensive amount of potential habitat on private land, it remains a priority to survey tortoise populations located on private land and ascertain that appropriate management plans are instituted to ensure the persistence of these populations.

The Howard Gilman Foundation privately owns White Oak Plantation (WOP), the site of my study. Historically, WOP has operated as a pine plantation, but today it is typically used as a meeting facility for various conventions. The White Oak Conservation Center, known for its captive breeding programs for endangered species, is also located on site. Moreover, several known gopher tortoise sub-populations inhabit the property, providing an excellent opportunity to study this species on private land.

Given that the gopher tortoise was placed on the candidate list for federal protection in 2011 and could remain there indefinitely, it is vital that all known populations be assessed to expedite the evaluation of the tortoise under the Endangered Species Act. My study contributes demographic, reproductive and growth data on a previously unstudied gopher tortoise population.

Objectives

The objectives of this study were to: 1) measure demographic parameters such as age class structure and density to determine viability of a previously unstudied gopher tortoise population; 2) assess the reproductive success of that population to determine recruitment levels; and 3) determine growth rates for each

of the age classes based on mark-recapture data. Age class structure has allowed me to compare this site to other studies on gopher tortoises and to ultimately assess the potential persistence of this population. Examining the reproductive biology of the population will reveal information on nest success and recruitment of hatchlings. These data are especially important due to the fact that isolated fragments of tortoise habitat can contain relic populations where recruitment is greatly reduced or is no longer occurring (Mushinsky et al., 2006; Schuster-Barber, 2009). Finally, few studies have been conducted on growth rates of gopher tortoises, specifically for the hatchling age class. More data are needed about this key developmental period in gopher tortoise life history and will be vital to better inform future management plans.

METHODS

Research Site

White Oak Plantation is located on 2,995 ha of pine woodland in northeast Florida, adjacent to the St. Mary's River that creates the border between Florida and Georgia. The property is composed of native longleaf pine forest, interspersed with regions of planted slash and sand pine that were used in WOP's previous commercial harvesting activities. The plantation also contains five known sub-populations of gopher tortoises. My study area consisted of two of the five native sub-populations, located in regions referred to as Site A and Site B (Fig. 1). The other three sub-populations were not studied.

Site A is approximately 19.18 ha and is comprised of longleaf pine (*Pinus palustris*) and turkey oak (*Quercus laevis*) throughout. Groundcover vegetation surveys revealed that coverage is primarily tailed bracken fern (*Pteridium aquilinum*), grasses such as wiregrass (*Aristida stricta*) and crabgrass (*Digitaria spp.*), and yellow jessamine (*Gelsemium sempvirens*) (N. Bayona, pers. comm.). Site A was last burned in 2005. Site B is a sandhill habitat of approximately 80.37 ha. Ground coverage at this site is more diverse than at Site A and is composed primarily of juvenile slash pine (*P. elliotti*), Elliot's milkpea (*Galactica elliotti*), crabgrass (*Digitaria spp.*) and sawtooth blackberry (*Rubus pensilvanicus*) (N. Bayona, pers. comm.). Site B was last burned in 2006 and before that in 1999; although

there is a burn plan that states this site should be burned every two to three years (J. Vaughn, pers. comm.).

Historically, WOP has suggested that these two sites support one continuous tortoise population, but as a dirt road with steep ditches maintained on both sides (to prevent flooding) divides the two sites, there actually is limited opportunity for migration of tortoises from one site to the other. The majority of Site B is comprised of a region completely void of tortoise burrows (referred to from here on as the intermediate region). I conducted a preliminary survey of the intermediate region in May 2010 and again in 2011. I found no evidence of tortoises or burrows in either survey. The ground cover in the intermediate region is dominated by thick stands of large gallberry (*Ilex coriacea*) with a few scattered juvenile slash pines. There are also ditches that run North-South and East-West throughout this region.

Data Collection

I. Burrow Survey

I conducted an initial burrow survey in May 2010. Prior to locating the burrows, I created transect corridors running north/south in the northern site (Site A) and east/west in the southern site (Site B). Each corridor was 25 m wide and of variable length. Following completion of the transect corridors, we (myself and my undergraduate field team) located burrows by walking along each transect at arm's length from one another while scanning for burrows. Upon locating a burrow, we

recorded its size (hatchling, juvenile, sub-adult or adult) and its occupancy status (active, inactive or abandoned). Burrow sizes were estimated visually, while burrow occupancy was estimated using categories outlined in Auffenberg and Franz (1982), which first described burrow occupancy status as active (appearing fresh with recent signs of tortoise activity), inactive (burrow entrance partially covered with debris but still intact) or abandoned (burrow collapsed or filled in with debris)(Fig. 2). After categorizing a burrow, we took its GPS coordinates and planted a small, numbered stake directly to the right of the burrow mouth. We continued to mark burrows throughout the study (daily from May-October of 2010 and 2011) that may not have existed when the initial burrow survey took place.

II. Nest Survey

In northern Florida, gopher tortoises generally oviposit from mid-May through the end of June (Landers et al., 1980; Smith, 1995; Butler and Hull, 1996; Mushinsky et al. 2006). Upon completion of the burrow survey, the remainder of May and the entirety of June were spent searching for tortoise nests. Female tortoises often lay their eggs in a pile of sand outside the burrow mouth known as the apron (Landers et al., 1980; Wright, 1980; Butler and Hull, 1996). In both May 2010 and 2011, I compiled a list of all active adult burrows within both sites and searched their burrow aprons for eggs. At each burrow, a 1m² section of chicken wire was spread across the apron and a wire survey flag was used to probe each hole of the chicken wire (Smith, 1995; Butler and Hull, 1996). Upon feeling contact with an object, we dug down with our hands until we located the object. When we

discovered a clutch, we carefully removed each egg and immediately marked a black dot on the top of each egg so as not to shift its orientation. We then measured each egg's length and width with calipers (as gopher tortoise eggs are not perfectly spherical) and its mass using a 1kg Pesola scale. Eggs were then replaced into the nest cavity and re-buried. We secured a hardware cloth cage over the nest with tent stakes to both protect the nest from predators and to contain the hatchlings upon emergence. Nests were monitored daily for the remainder of the field season until hatching occurred. When eggs hatched, we counted, measured and weighed the hatchlings and then released them at the site, noting the distance at which they stopped to begin digging a burrow or bury themselves in the sand.

III. Tortoise Survey

In order to characterize the demography of the gopher tortoises at WOP, we trapped, measured, weighed and marked the tortoises at Site A and Site B. Foraging and basking tortoises were captured by hand when possible, but the majority of tortoises were caught using pitfall bucket traps placed outside the burrow mouths (Cox et al., 1987; Breininger et al., 1991).

We constructed the bucket traps by digging large holes in burrow aprons directly in front of burrow mouths (Cox et al., 1987). Nineteen-liter buckets were used for adult burrows, 10.5 L flowerpots for sub-adult burrows and 5.5 L flowerpots for juvenile burrows. Hatchling burrows were never equipped with traps. Once we placed the buckets into the ground, we covered them with a light layer of newspaper and camouflaged the surface with pine needles and other leaf

debris. We left a damp sponge inside each trap to prevent trapped tortoises from dehydrating. All buckets and flowerpots had drainage holes at the bottom so tortoises would not drown in the traps during heavy rainfall. Traps were set each morning and closed each evening as requested by WOP personnel. We trapped during the active season (from May through October of 2010 and 2011), with the exception of mid-May to the end of June, which coincided with nesting season. We did not employ bucket traps in aprons of burrows that had already been fitted with nesting cages.

We set approximately eight traps each day and attempted to equalize the number of adult, sub-adult and juvenile traps set over the course of the season. Once we captured a tortoise in a given trap, we closed that trap and constructed another trap at a different active burrow. Upon capture, we measured each tortoise's carapace length (CL) and width (CW), plastron length (PL), shell height (H), and total length (TL) using hand-held calipers. We used dial calipers for hatchling and juvenile tortoises, and larger tree calipers for sub-adult and adult tortoises (Moore et al., 2009). We then weighed the tortoises using handheld Pesola scales. Large tortoises had a belt fitted around their mid-section that was suspended from a 10kg scale, while small tortoises were briefly placed in an open Ziploc bag and suspended from a 1kg scale. Adult tortoises are sexually dimorphic and were sexed by identifying key morphological differences, such as plastral concavity and length of the gular scute projection (McRae et al., 1981). We individually marked tortoises by drilling a specific pattern of small holes into the marginal scutes of the carapace (Cagle, 1939). We then assigned the tortoises to age

classes based on their CL measurements. Individuals longer than 220mm were considered to be adults, individuals between 120-220 mm in length were classed as sub-adults, individuals between 60-120 mm long were called juveniles, and hatchlings measured between 40-60 mm. Size parameters were modeled after those used in Landers et al. (1980) and Diemer (1986). When a tortoise was recaptured at any time during the season, we recorded updated size and weight measurements.

Gopher tortoises were also visually examined for presence of gopher ticks, symptoms of upper respiratory tract disease (URTD) and bot fly (*Cistudinomyia cistudinis*) infections. We primarily looked for gopher ticks and bot fly infections at the base of each limb of the tortoise, and we looked for URTD symptoms on the face of the tortoise – noting any mucous discharge from the nostrils or swollen eyelids (Jacobsen et al., 1991). If any of these ailments were observed, we recorded them on the data sheet for that particular tortoise.

I determined gopher tortoise abundance by capturing as many tortoises as possible using both bucket trapping and hand capture techniques. Population abundance is often estimated by multiplying a correction factor of 0.614 (Auffenberg and Franz, 1982) by the number of active and inactive burrows. Burrow correction factors are used as population estimates due to the secretive nature of the gopher tortoise and its propensity to spend the majority of the day in its burrow (Wilson et al., 1994; Nomani et al., 2008). Because burrow occupancy changes both temporally and spatially (Breininger et al., 1991; McCoy and Mushinsky, 1992), I created a correction factor unique to the data I collected at

WOP. After we substantially surveyed both sites in this study, I used the number of marked tortoises to calculate a suggested correction factor for WOP. I divided the number of tortoises at WOP by the number of active and inactive burrows to produce the new site-specific correction factor.

IV. Growth

A short-term growth analysis was performed for all recaptured tortoises during the two-year study at WOP. I calculated growth rates for 23 recaptured individuals, including seven adults, three sub-adults, six juveniles and seven hatchlings. Because the growth data were collected each time a tortoise was recaptured, the amount of elapsed time between initial and final measurements for each individual was different. Therefore, the data were adjusted to estimate growth rates for all recaptured individuals in mm/year. For the majority of the individuals in the juvenile, sub-adult and adult age classes, the initial and final measurements were taken nearly a year apart and sometimes more than a year apart, so less extrapolation was needed to report the growth rates. However, all but one individual in the hatchling age class had measurements less than 3 months apart, thus a higher degree of extrapolation was used to determine growth rates for hatchlings. I calculated the growth rates as growth per day (mm) and then converted them to annual growth rates. Pike (2006) used a similar method except that daily growth rate was converted into a six-month growth rate rather than an annual growth rate. I used CL for the growth measurements, as it is the parameter most often used in growth analysis (Landers et al., 1982). Additionally, using CL

reduces variability while measuring male and female adult tortoises, as the more elongated gular projection in males is not taken into account.

Data Analysis

I established a site-specific correction factor, offering a comparison to the widely-implemented 0.614 correction factor used by Auffenberg and Franz (1982) and others proposed since then (Breininger et al., 1991). I did this by dividing the total number of tortoises by the combined number of active and inactive burrows. I calculated the correction factor after the completion of the second field season in 2011, when I believed there were a sufficient number of captured tortoises to do so (McLaughlin, 1990).

As in most field studies, data were not normally distributed and therefore non-parametric tests were used. Chi-square contingency tables for association were used to compare Site A and Site B for significant differences in male-to-female sex ratios, burrow occupancy and size distributions, and age class structure. A Chi-square goodness-of-fit test was used both to determine if there was a significant deviation from the expected 1:1 sex ratio of adult tortoises and to assess significant differences in population sizes between the two sites. Size classes were converted to smaller intervals to generate a histogram displaying the percentage of tortoises belonging to each of the smaller size increments (Diemer, 1992). This adjustment was done primarily to identify small periods of time where tortoise recruitment may have been low or predation may have been high. Mann Whitney U-tests were

used to determine differences in adult CL between sexes and between sites (Diemer, 1992). The Kruskal-Wallis analysis of variance was used to determine significant differences in growth rates between the four age classes: hatchling, juvenile, sub-adult and adult. A univariate ANOVA (with Tukey's post-hoc and Bonferonni corrections) was performed across the four age classes to determine whether the aforementioned parameters of each age class accurately illustrated them. All tests were performed using SPSS software.

RESULTS

Burrow Survey

I recorded 312 tortoise burrows throughout both study areas at WOP; 236 at Site A and 76 at Site B. Number of burrows across sites varied significantly ($X^2 = 81.5$, $df = 1$, $p < 0.001$). Of the 312 burrows, 29.4% were adult burrows, 17.9% were sub-adult burrows, 42.6% were juvenile burrows and 5.8% were hatchling burrows (Fig. 3). Burrow size distribution differed significantly between sites ($X^2 = 13.247$, $df = 3$, $p < 0.005$); Site A contained a much higher percentage of juvenile burrows (50.2% of Site A burrows were juvenile burrows, while only 27.6% of Site B burrows were juvenile burrows), while Site B contained a higher percentage of adult burrows (43.4% of Site B burrows were adult burrows, while only 26.5% of Site A burrows were adult burrows). No burrows were ever located in the intermediate region (technically a portion of Site B).

I classified 74.5% of burrows as active, 11.6% as inactive and 13.6% as abandoned (Fig. 4). The proportion of active, inactive and abandoned burrows did not differ significantly between Site A and Site B ($X^2 = 1.35$, $df = 2$, $p > 0.05$).

Population Structure

We captured and marked a total of 109 gopher tortoises at WOP: 86 at Site A and 23 at Site B (Table 1), resulting in tortoise densities of 4.48/ha at Site A and

1.15/ha at Site B. This resulted in a suggested site-specific correction factor of 0.406 (the total number of tortoises divided by the number of active and inactive burrows). When separately analyzed at each site, the correction factor was 0.441 at Site A and 0.354 at Site B, which did not differ significantly from one another ($X^2 = 0.01$, $df = 1$, $p > 0.05$).

Other demographic studies have reported gopher tortoise population structure data as three age classes: juvenile, sub-adult and adult (McRae et al., 1981; Diemer, 1992; Rostal and Jones, 2002). I chose to analyze age structure with and without the hatchling age class (Table 2), so that I could more easily compare my data with that of other studies in which the hatchling age class was not included (McLaughlin, 1990).

Of the marked tortoises at WOP, 29 (26.6%) were adults, 17 (15.6%) were sub-adults, 39 (35.8%) were juveniles and 24 (22.0%) were hatchlings (Fig. 5). Both hand-caught hatchlings and those that emerged from marked nests were combined to calculate the overall hatchling number reported. When hatchlings were not included in the population structure, there were 45.9% juveniles, 20.0% sub-adults and 34.1% adults. Age class distribution varied significantly between Sites A and B when the hatchling age class was included ($X^2 = 8.14$, $df = 3$, $p = 0.043$), but not when hatchlings were discounted ($X^2 = 2.47$, $df = 2$, $p = 0.291$). Site A had significantly more tortoises than Site B ($X^2 = 36.42$, $df = 1$, $p < 0.001$). Site A had also had a higher percentage of hatchlings and juveniles than Site B. Overall, there were a higher

percentage of juveniles at WOP than any other age class. Both sites had very few sub-adults, particularly those with CLs between 160-220 mm (Fig. 6).

Adult male tortoises had a mean CL of 263.8 mm (range = 235-287 mm, SD = 15.1 mm), while adult female tortoises had a CL of 269.6 mm (range = 246-280 mm, SD = 12.8 mm). Mean CL was not significantly different between sexes ($U_A = 74.5$, $p = 0.371$). Adult tortoises from Site A had a mean CL of 265.5 mm (range: 235-289 mm, SD = 16 mm), and adult tortoises from Site B had a mean CL of 267.3 mm (range: 252-282 mm, SD = 10.5 mm). Mean CL was not significant between sites either ($U = 91.5$, $p = 0.768$). The sex ratio of adult tortoises at WOP was 1:1.55 (F:M), which is not a significant deviation from the expected 1:1 ratio ($X^2 = 1.69$, $df = 1$, $p = 0.194$). The sex ratio between sites was also not significantly different than expected ($X^2 = 0.31$, $df = 1$, $p > 0.05$). Mean CLs for all four age classes are as follows: hatchlings (including both hand-caught and those which emerged from nests) – 50.6 mm; juveniles – 91.9 mm; sub-adults – 171.2 mm and adults – 266.1 mm. Mean CL between age classes is significantly different (ANOVA = 687.04, $df = 3$, $p < 0.0001$).

Reproduction and Hatchlings

We located a total of six nests during the study - four in 2010 and two in 2011. Mean clutch size was 3.8 eggs (range 2-7) over the entire study ($\bar{X} = 5$ in 2010, $\bar{X} = 2$ in 2011). One of the 2010 nests was discovered in September after a presumed depredation event; we recorded three intact eggs and re-buried them. As

we were unable to determine the total clutch size prior to the depredation, this nest was not included in average clutch size calculations. All nests were located within Site A for both years of the study.

Mean depth to the top of the nest cavity (i.e. distance to the uppermost egg) was 10.23 cm (6.1-14.35, n = 2) and the mean depth to the bottom of the nest cavity was 14.53 cm (10.45-21.6, n = 3). Mean egg diameter was 40.1 mm (34.2-43.5 mm, n = 20) and mean egg mass was 40.4 g (30.0-44.0 g, n = 18; Table 3).

Hatching success was 100% for all nests located in 2010, not including the depredated nest located late in the season. Two of the three remaining eggs in the depredated nest hatched. Hatching success in 2011 was 50%; all eggs hatched in one nest, while none hatched in the other. Upon release from the nesting cages, tortoise hatchlings dispersed an average of 1.83 m before stopping to dig a temporary pallet, bury themselves under pine needles and leaf litter or enter the parent burrow. Three hatchlings immediately began to forage upon release (Fig. 7).

We located 12 hatchling-size tortoises during June 2011, two of which had a visible egg tooth, had CL's of 44.5 and 47.0 mm each and had bright yellow coloration characteristic of young neonate hatchlings. The other 10 hatchlings had a mean CL of 54.6 mm and did not have egg teeth. These 12 hatchlings did not come from caged nests, and all were discovered while they were foraging outside of their burrows.

Growth

From the growth data compiled from mark-recapture data throughout the study (Fig. 8), I determined that adult tortoises at WOP have a mean growth rate of 1.64 mm/yr and sub-adults have a mean growth rate of 7.70 mm/yr. Juveniles grew faster and showed a mean growth rate of 9.28 mm/yr, while hatchlings had an even more rapid growth rate of 24.22 mm/yr. Growth rates for each age class deviate significantly from each other ($H = 13.267$, $df = 3$, $p = 0.004$). Mean annual growth rate showed a logarithmic relationship with CL, and slowed as CL increased ($R^2=0.49$).

Disease

No tortoises were observed to have gopher ticks or any symptoms of URTD (upper respiratory tract disease) at WOP. Two adult male tortoises were observed with bot fly (*Cistudinomyia cistudinis*) infections (S. Citino, pers. comm.). One of the two tortoises was recaptured in September 2011 and no longer had the bot fly infection.

DISCUSSION

Burrow Survey

Prior burrow surveys at these two sites reported a total of 301 burrows in 2006 and 257 burrows in 2008 (J. Vaughn, pers. comm.). The number is thought to have decreased due to increased groundcover in the years following the prescribed burn in 2006, making it more difficult to locate small juvenile and hatchling burrows (J. Vaughn, pers. comm.). By the conclusion of this study in 2011, 312 burrows were located; an increase of 55 burrows since the last survey in 2008. Neither site has been burned since 2006, so the increased leaf litter in the several years after the burn may not be the reason for the decreased number of burrows in 2008. However, it must be noted that I discovered many hatchling burrows by following hand-caught hatchlings to their burrow entrances upon release.

The percentage of active burrows has remained consistent since the survey in 2008; however the percentage of inactive burrows decreased from 17.9% to 11.6%, while the percentage of abandoned burrows increased from 5.8% to 13.6%. This could either be a result of discrepancies that arise when different researchers attempt to classify burrows based on external characteristics (Smith et al., 2005), or the number of abandoned burrows is actually increasing. If the number of abandoned burrows is increasing, it is likely because canopy cover percentage is too

high due to the absence of prescribed burns over the last six to seven years at these sites. N. Bayona (pers. comm.) reported canopy coverage estimates of 88.9% at Site A and 85.3% at Site B in June 2011, indicating that little sunlight is reaching the forest floor. The habitat requirements devised by the Florida Fish and Wildlife Commission (FWC) state that acceptable gopher tortoise habitat should have below 60% canopy coverage, while desirable tortoise habitat should have below 40% canopy coverage (FWC, 2008). Thus, the tortoises at WOP may be abandoning previously sunlit burrow sites in search of new ones. Differences in number of burrows or burrow occupancy ratios between Site A and Site B are not known from years prior to this study, as WOP has historically managed these two sites as one continuous population.

Currently, Site A contains significantly more burrows than Site B, despite being of comparable size (when the intermediate region of Site B is not included). There remain no burrows within the intermediate region, which signifies that this region is currently inhabitable by gopher tortoises. Due to lack of available data prior to 2005 (when WOP began conducting burrow surveys), it is unclear when this region, if ever, was last occupied by tortoises.

Correction Factor

My site-specific correction factor of 0.406 is considerably lower than the widely used 0.614 correction factor proposed by Auffenberg and Franz (1982). It

has been suggested that 0.614 might overestimate the number of tortoises in a population (Breininger et al., 1991). McCoy and Mushinsky (1992) reported that in 22 of 26 study sites, the 0.614 correction factor greatly overestimated the number of tortoises in each population. My correction factor of 0.406 might slightly underestimate the tortoise population if there were some tortoises we failed to capture during the two-year study; however, burrow sharing was commonly observed, both through capturing multiple individuals in the same bucket trap or by observing up to three adult individuals together in the mouth of a burrow. Tortoises were also recorded occupying up to five different burrows throughout the study. Whenever possible, it is beneficial to create a site-specific correction factor, so that tortoise numbers are not overestimated (Breininger et al., 1991; Diemer, 1992). The usage of Auffenberg and Franz's 0.614 correction factor can lead to an inflated estimate of gopher tortoise abundance and result in misconceptions affecting the management of this species.

Population Structure

Overall population structure indicates high levels of recruitment, as hatchlings and juveniles comprised 57.8% of the total population (46.8% when discounting hatchlings that emerged from protected nests). My study has examined a population of tortoises in which there was a higher percentage of juveniles than sub-adults or adults, unlike many other demographic studies conducted throughout the gopher tortoise's range (McRae et al., 1981; McLaughlin, 1990; Diemer, 1992;

Rostal and Jones, 2002). Not only were juvenile and hatchling tortoises numerous relative to the sub-adult and adult age classes, they were also easy to locate. I was able to successfully recapture hatchlings several times without the use of bucket traps or radio telemetry, which suggests that they spent considerable time outside their burrows, as previously noted by Pike and Grosse (2006). Within the study area, this observation primarily refers to Site A, as only seven juveniles and one hatchling were located in Site B.

It should be noted that the percentage of hatchlings among the WOP tortoise population (22.0%) was higher than the percentage of hatchling burrows (5.8%). This finding suggests that previous studies using only burrow counts to estimate tortoise abundance may have underestimated hatchling survivorship. We found that hatchling burrows are small, inconspicuous, often concealed underneath shrubs and grasses, and therefore easy to overlook (Alford, 1980; Diemer and Moore, 1994, Mushinsky et al., 2006). Pike (2006) also reported that hatchling burrows are surrounded by a high percentage of groundcover (81.4%) and tall vegetation greater than 50 cm in height.

The percentage of sub-adult tortoises at WOP was lower than all other age classes; a phenomenon that was also observed in many other large-scale demographic studies conducted throughout the gopher tortoise's range (McRae et al., 1981; Diemer, 1989; McLaughlin, 1990; Rostal and Jones, 2002). Therefore, it does not seem likely that a single climatic event occurred that prevented survival of the current sub-adult cohort at WOP. Low sub-adult abundance may be more

expected in the aforementioned studies, as they also reported low numbers of juveniles. However, WOP has high percentages of both hatchlings and juveniles, which suggests that graduation to the sub-adult age class is probable.

Female to male sex ratio (F:M) was similar to the ratios reported in other studies (McRae et al., 1981; Diemer, 1989). My calculated ratio did not significantly deviate from a 1:1 expected ratio as it did in both McRae et al. (1981) and Diemer (1989), but this may be due to smaller sample size ($n = 28$). Mean CL between adult male and female tortoises was not significantly different either, which is surprising given that female gopher tortoises tend to attain larger sizes than males (Landers et al., 1982).

Site B contained fewer tortoises than Site A, as well as a smaller percentage of young tortoises. While the majority of Site B was comprised of thick gallberry vegetation and void of tortoises (in the intermediate region), there remain approximately 20 ha of suitable habitat for resident tortoises. This portion of Site B contains roughly the same area as Site A, yet Site A supported 86 tortoises while Site B supported only 23 tortoises. Additionally, only one hatchling was found at Site B, while the remaining 23 hatchlings were found at Site A. No nests were found at Site B throughout the study, while six were located at Site A. It is evident that Site A is experiencing much higher levels of recruitment than Site B. Throughout both years of the study, no tortoise captured at one site was ever recaptured at the other site, indicating that the sub-populations are not interacting or experiencing gene flow. A telemetry study, however, could provide a more definitive answer about whether or

not tortoises travel between sites or are restricted to only one site. Interaction between Site A and Site B tortoises could be prevented by the combined barriers of dense vegetation in the intermediate region and the deep ditches on either side of the dirt roads dividing the two sites.

One tortoise, an adult female, was found dead during the study. Her carapace was smooth and well worn, which is indicative of an older animal. There were no visible injuries, nor was there evidence of illness, and the necropsy report concluded that the cause of death could not be identified (S. Citino, pers. comm.). Predation was also not observed at either Site A or Site B, aside from an uncovered nest that was discovered in September 2010 and believed to have been partially depredated. As this nest was discovered after a rainstorm, any predator tracks may have been washed away.

Reproduction

Nest sample size for the tortoise population at WOP was low for both years of the study, but exceptionally low in 2011 (n=4 in 2010, n=2 in 2011). Clutch size also decreased from 2010 (\bar{X} =5) to 2011 (\bar{X} =2). Mean clutch size across both years was 3.8; lower than mean clutch size reported by any other study in Florida and Georgia (Table 3). The only study that reported an equal mean clutch size was conducted in South Carolina (Wright, 1982), representing the northernmost region of the gopher tortoise's range where smaller clutch sizes would be expected. This result could simply be due to a limited nest sample size, or it could be a result of

smaller reproducing females that are less fecund than larger females in other regions (Landers et al., 1980). Mean CL for female gopher tortoises at WOP (269.6 mm) is shorter than what has been reported in many other studies to date: in Mitchell (2005), mean female CL was 302.2 mm in southern Georgia; at two sites in south Georgia studied by Rostal and Jones (2002), mean female CL was 290 and 306 mm; Landers et al. (1980) reported a mean female CL of 283 mm in southwestern Georgia, and Ashton et al. (2008) reported mean female CLs of 274 and 308 mm at sites in south and south-central Florida, respectively. There exists a geographic cline in maximal size attained by adult gopher tortoises, which is correlated with the length of the growing season and productivity (Ashton et al., 2008). Given this pattern, WOP female tortoises should be attaining sizes similar to those reported from southern Georgia and northern Florida. As WOP females appear to be undersized, clutch size may be reduced as a result.

Ninety-five percent of eggs hatched in 2010, while only 50% hatched in 2011. This discrepancy is partially due to the fact that an entire clutch from one nest did not hatch in 2011. Across both years of the study, mean egg hatching success was 87.5%, which is consistent with other studies conducted in Florida and Georgia (Table 3). Mean hatchling CL (46.8 mm) was also comparable to that reported in other reproductive studies (Table 3).

During this study, every nest was located in Site A. Despite low sample size, there are implications as to why nests were never found in Site B. Female gopher tortoises require direct sunlight for nesting (Landers and Buckner, 1981), as the

eggs rely on the warmth from the sun to incubate. Therefore, high canopy coverage coupled with dense mid-story and ground vegetation could be partially responsible for the lack of nests at Site B (N. Bayona, pers. comm.).

Sampling effort for nest location was consistent over both years; all active adult burrows were probed throughout late May and the entire month of June. Hatchling tortoises were commonly encountered while surveying the study area and represented 22% of all located tortoises (11% when those that hatched from caged nests were not included). The common hatchling sightings coupled with the low number of nests located suggests that the nest-probing method we used may not be the most effective technique for locating nests. One possible problem with the nest-probing method was that many burrow mounds at WOP had hard-packed sand, and it was sometimes difficult to safely penetrate the sand with the wire probe.

While there is climatic variation in the timing of the nesting season across the gopher tortoise's range, studies in north Florida and southern Georgia have reported the nesting season to occur from mid-May to mid-June (Iverson, 1980; Landers et al., 1980; Diemer, 1989; Butler and Hull, 1996; Mushinsky et al., 2006). The gopher tortoise incubation period is approximately 80 to 90 days in Florida (Iverson, 1980), which translates to hatchling emergence dates of August through October. The two neonates that I discovered foraging outside of their burrows on 19 June and 20 June 2011 were both within the CL range for hatchlings that emerged from caged nests during this study (CL of the two hatchlings = 44.5 mm and 47.0 mm; CL range of caged hatchlings upon emergence = 44.5-48.2 mm). Every

other hand-captured tortoise within the predetermined hatchling size parameters (40-60mm) was over 51 mm. The two hatchlings also possessed an egg tooth (Fig. 9), and showed traces of yolk sac plugs on their abdomens (Moore et al., 2009), indicating they were only days old (Arata, 1958). Furthermore, hatchling gopher tortoises have characteristically bright yellow shells (Mushinsky et al., 2006), as did these two individuals. Therefore, it appears that these two tortoises hatched several months earlier than the August-October emergence period reported by other studies done in Florida and in southern Georgia (Hallinan, 1923; Iverson, 1980; Landers et al., 1980; Butler and Hull, 1996; Pike and Seigel, 2006). Taylor (1982) described several female tortoises in north-central Florida that were found to be carrying oviductal eggs in April, suggesting that hatching would occur in June or July. McLaughlin (1990) observed young-of-the-year hatchlings throughout the year at Sanibel Island in south Florida, and suggested that the gopher tortoise nesting season may not be as well-defined as previously suggested. Also, Moore et al. (2009) reported several females with calcified eggs in April and year-round presence of neonate hatchlings at their study site in southeastern Florida.

Although WOP is located in northern Florida, in a climate that is less tropical than that of the south Florida studies in which eggs hatched in early summer, it is still possible that the nesting season in north Florida begins earlier than mid-May. My study has produced the first documented observation of neonate hatchlings in June in north Florida.

Growth

Hatchling growth rates for this study are considerably higher than reported by recent studies (Pike, 2006). From mark-recapture data obtained from June through October 2011, hatchlings at WOP (n=7) had a mean growth rate of 24.22 mm/yr (range: 13.14-32.38 mm/yr). Pike (2006) reported a mean six-month hatchling growth rate of 3.01 mm, which converts to an annual mean growth rate of 6.02 mm/yr (range: 0.76-12.08 mm/yr). In southern Georgia, Landers et al. (1982) reported a mean annual growth rate of 13 mm/yr for tortoises with an initial CL length of 50-59 mm (range: 7-20 mm/yr, n=15), and Goin and Goff (1941) reported an annual growth rate of 11 mm/yr for a single hatchling (n=1) in central Florida. Another study in Florida (Mushinsky et al., 1994) reported the mean annual growth rate most similar to my study (18.9 mm/yr), but this was for individuals estimated to be between one and 11 years of age based on annuli counts. So, while this is not a true estimation of the hatchling size class, it suggests more rapid growth rates in the early life stages of the gopher tortoise than other previous studies do, as I have also found.

The extraordinary growth rate of hatchlings in this study may be related to a few unusual circumstances characteristic of the environment at WOP. First, hatchlings may be benefitting from high forage quality at Site A (N. Bayona, pers. comm.); where 21 of 22 hatchlings were recorded. Hatchlings also tend to spend more time outside of their burrows than do juveniles (Pike and Grosse, 2006),

giving them more time to forage and grow. Foraging activities can be conducted with a reduced chance of mortality due to the improbability of encountering predators at WOP. Raccoons, a top predator of young gopher tortoises, were never observed at either Site A or Site B during the study. While there are many other documented predators of hatchling tortoises, such as various snakes and birds of prey, mammals (the majority of which were believed to be raccoons) were responsible for 70% of hatchling deaths in a north Florida study by Butler and Sowell (1996). Artificially high raccoon abundance is common in habitats in close proximity to developed areas (Smith and Engeman, 2002), and WOP does not represent a habitat influenced by anthropogenic activities. Thus, hatchling activity and survival may be promoted by the absence of key predators at WOP, and with increased foraging activity comes more rapid growth.

My growth data also represents the variability among individual tortoises. While the general trend of tapered growth with age is evident (see Figure 8), it should be noted that there are exceptions. Six of seven adult tortoises experienced little to no growth during the study, but one adult grew as rapidly as some of the juvenile tortoises. This observation was described in Landers et al. (1982) as well, when they described a Florida gopher tortoise with a 60mm/yr growth rate; approximately twice as rapid a growth rate as shown by the fastest-growing individual at their study site in Georgia. Young adult male tortoises may experience spurts of rapid growth at the onset of sexual maturity (D. Rostal, pers. comm.), which may account for the one male tortoise that was growing at a much faster rate.

Disease

While the only ailments observed for WOP gopher tortoises were parasitic larval bot fly infections, it is still possible that URTD is present in the population. I was only able to visually examine each tortoise for known URTD symptoms, but no blood work was actually conducted to determine presence of antibodies. While studies on both desert tortoises and gopher tortoises have concluded that presence of nasal discharge is the most reliable indicator of URTD (Schumacher et al., 1997; Wendland, 2007), it must be noted that tortoises infected with URTD only experience nasal discharge intermittently. Diemer et al. (2010) reported that nasal discharge was only observed in six percent of tortoises, even though 88% of tortoises showed one or more clinical signs of URTD at some point during their four-year study. More data is needed to ensure the presence or absence of URTD at WOP.

Management Implications

I believe that the health and stability of both WOP tortoise sub-populations (particularly Site B) could be improved by a management approach that attempted to make both sites easily accessible to all tortoises in both sub-populations. Small populations are more vulnerable to extirpation than large populations, either through inbreeding, predation, competition for resources or spread of infectious disease, so it is particularly important to increase tortoise numbers in the Site B population. Using radio-telemetry to track tortoises, Eubanks et al. (2002)

determined that the minimum area required to sustain 50 adult tortoises was 25-81 ha. McCoy and Mushinsky (2007) estimated that the minimum patch size for gopher tortoise populations is over 100 ha. At WOP, Site A is 19 ha, and the area of Site B without the intermediate region is 20 ha. Both of these sites contain less than the minimum area recommended by the two aforementioned studies. If efforts were made to merge these two sub-populations, their combined area would be within the acceptable range (39 ha for these two areas alone, and approaching 100 ha if the intermediate region of Site B was converted into viable tortoise habitat).

Beyond increasing the available range of tortoises from Site B, I believe that tortoises from Site B would benefit greatly from interaction with those from Site A. Currently, the Site B sub-population is small and experiences little to no recruitment. Site B tortoises have virtually no possibility of expanding their territories, and thus are effectively isolated in a small fragment of viable habitat, which may be a factor in their limited population growth. There are several actions in the form of habitat restoration that can be taken to ensure these two sub-populations are able to interact.

First and foremost, a burn program should be designed and consistently implemented. According to WOP personnel, a burn plan was created and maintained for several years, but in recent years, the burn team was disbanded for financial reasons. Site A has not been burned since 2005 and Site B since 2006. In pine flatwoods, it is recommended that summer prescribed burning should occur every two to five years and in sandhill communities, every two to seven years

(Mushinsky et al., 2006). To produce sufficient tortoise forage and allow unimpaired travel between sites, it is mandatory that a burn protocol be part of the management of all plots occupied by gopher tortoises.

Second, I highly recommend the mechanical removal of gallberry in the intermediate region. Due to the prevalence and density of gallberry in this region, prescribed burning alone may not relieve the problem. In its current state, the intermediate region is neither accessible nor easily utilized by gopher tortoises. Improvement of the intermediate region is crucial to the health and viability of the gopher tortoise population because it is the area that most directly connects Site A to Site B; in the intermediate area's current state, migration of gopher tortoises between the two sites is highly unlikely. Although WOP has indicated that it has future plans to restore this region to a longleaf pine ecosystem by removing most of the gallberry (S. Shurter, pers. comm.), it is not clear when this will occur. If the intermediate region is more effectively managed, the likelihood that the two gopher tortoise sub-populations will effectively merge will increase.

Third, I recommend that the steep ditches on either side of all dirt roads intersecting Sites A or B should be filled in, as they create a geographic roadblock that most tortoises cannot cross. I observed a sub-adult attempt to transverse one of these ditches and become stuck at the bottom of the ditch. I am convinced that these ditches impede travel by tortoises between the two sites. Eliminating barriers between the two sites could ultimately increase genetic diversity and allow the tortoises to establish larger territories and foraging ranges.

I have no recommendations to modify the usage of dirt roads at WOP. During my study there were no instances in which tortoises were injured or killed by vehicular traffic. The dirt roads within WOP are infrequently used, as front gate personnel regulate access to the roads 24 hours a day. Those who do gain access are asked to maintain slow speed limits and to not disturb captive or wild animals. Additionally, signs informing drivers of the presence of tortoise habitat are adequate. Thus, road mortality does not appear to be a great risk to WOP gopher tortoises.

Conclusions

Demographic and reproductive data suggest that Site B is experiencing low levels of recruitment, while Site A is likely a healthier and more robust population as evidenced by the higher number of tortoises – specifically hatchlings and juveniles. Hatchlings at Site A had significantly faster annual growth rates than other studies reported throughout the gopher tortoise's range. Hatchlings may also be emerging from nests several months earlier than the known emergence period for north Florida, suggesting the possibility of nesting occurring earlier in the year than the documented nesting season which spans from mid-May through June.

While WOP considers Site A and Site B to hold one continuous population of gopher tortoises, it appears that geographic and vegetative barriers are preventing their interaction, and thus inhibiting gene flow. Both a periodic prescribed burn protocol and mechanical vegetation removal are suggested to control the dense

gallberry in the intermediate region that separates Site A and Site B. The steep ditches on the dirt roads bisecting these sites should also be removed, as they present a barrier to tortoises that attempt to cross the road.

FIGURES AND TABLES

Figure 1: Location map for White Oak Plantation. Research sites A and B are identified on the map. The darker box indicates the intermediate region of Site B. Data points represent tortoise burrows: blue = adult, yellow = sub-adult, pink = juvenile and green = hatchling).

Map redacted. Paper copy available upon request to home institution.

Figure 2. Photos of the three burrow occupancy states: (A) active burrow, (B) inactive burrow and (C) abandoned burrow.



(A)



(B)



(C)

Figure 3. Burrow size distribution at WOP. Burrows were divided into four sizes- hatchling, juvenile sub-adult and adult.

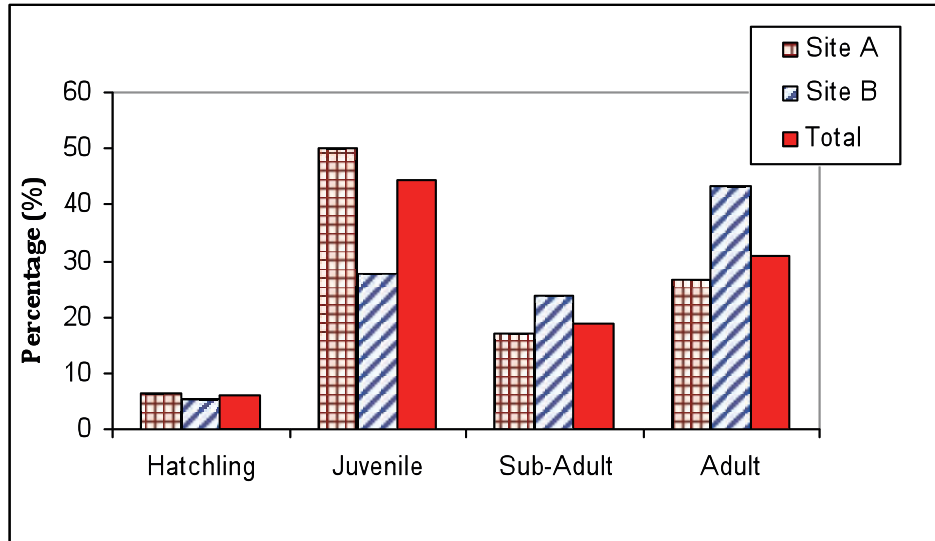


Figure 4. Burrow occupancy at WOP. Burrows are divided into three occupancy states: active, inactive and abandoned.

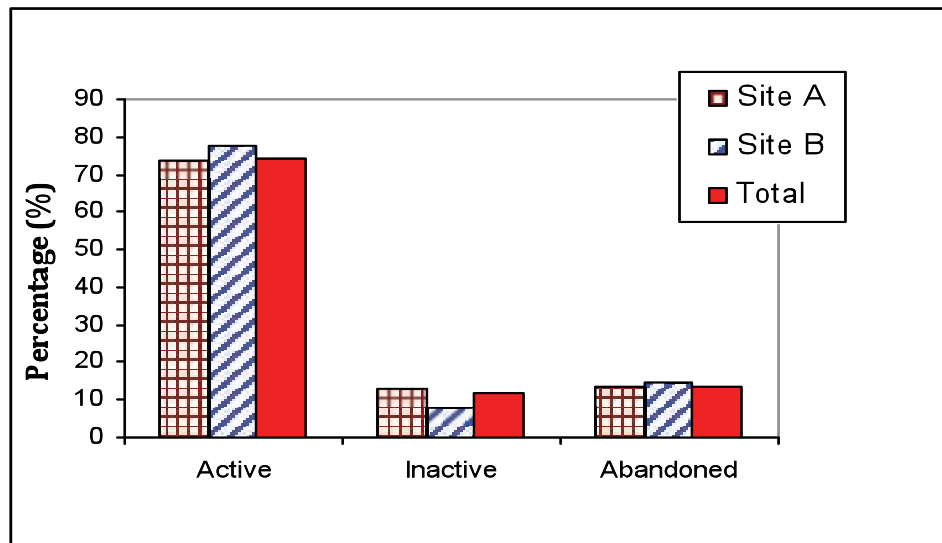


Figure 5. Gopher tortoise age class structure at WOP.

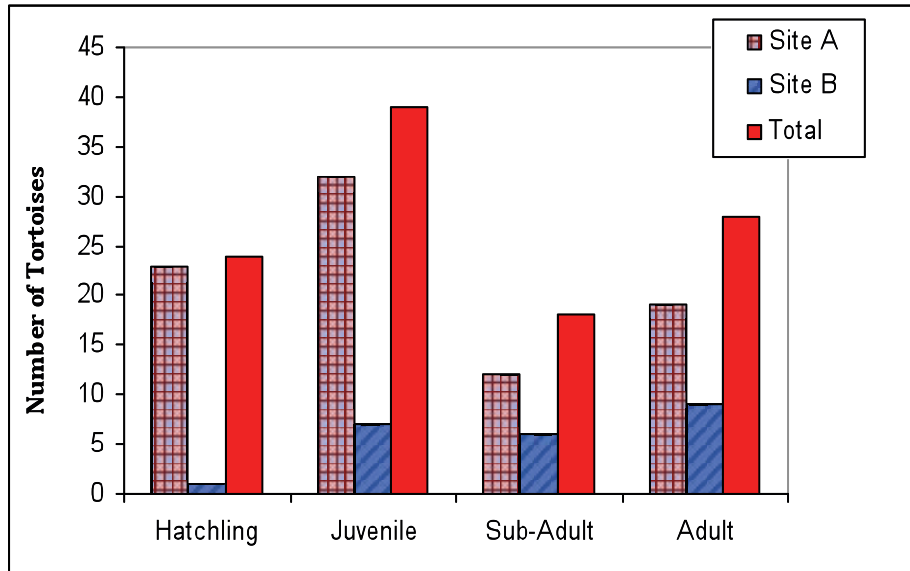


Figure 6. Histogram of tortoise CL distribution at WOP. Size intervals are 2 cm each. Interval 4-6 cm includes hatchlings from caged nests - when those are not included, this interval would contain 12 individuals.

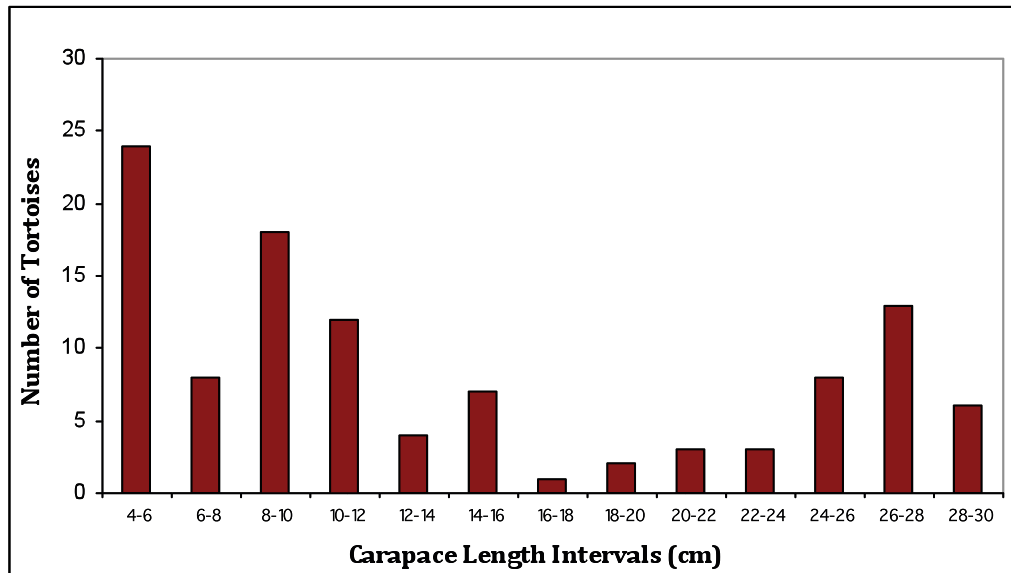


Figure 7. A WOP hatchling engaging in foraging behavior immediately following release from a caged nest.



Figure 8. Annual growth rate of individual tortoises in relation to initial CL. The R^2 value is 0.49 when the outlier is included and 0.69 when the outlier is removed.

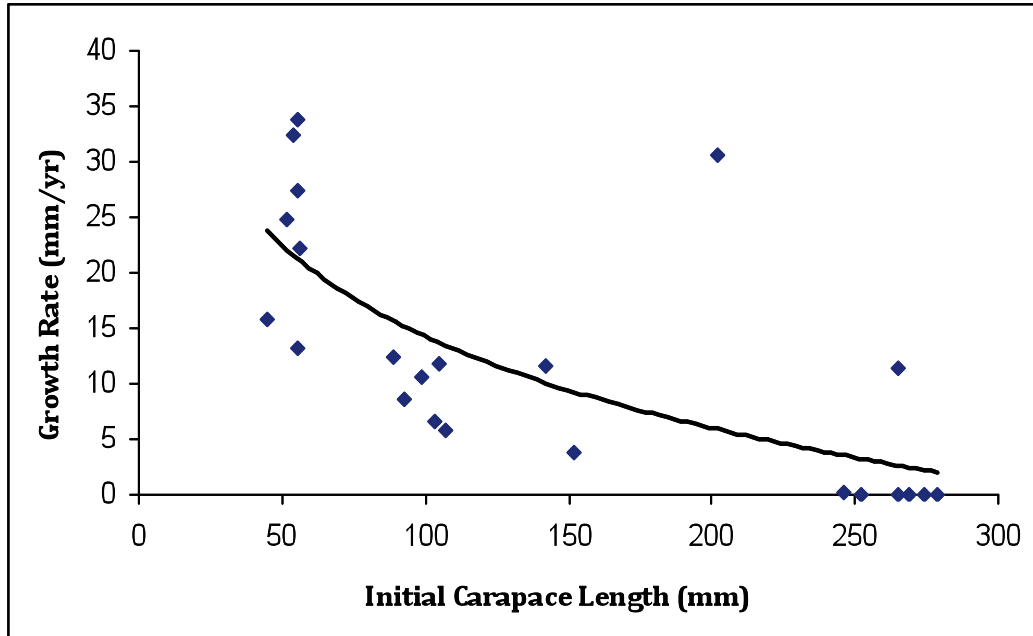


Figure 9. (A) Three hatchlings located on June 19, 2011. The center hatchling measured 44.5mm CL. (B) The same hatchling as seen in the center of the top picture, with full view of the egg tooth.



(A)



(B)

Table 1. Age class structure at WOP. Numbers (%) represent all tortoises either hand-caught or bucket-trapped at Sites A and B.

AGE CLASS STRUCTURE	SITE A	SITE B	TOTAL
HATCHLING	23 (26.7)	1 (4.3)	24 (22.0)
JUVENILE	32 (37.2)	7 (30.4)	39 (35.8)
SUB-ADULT	11 (12.8)	6 (26.1)	17 (15.6)
ADULT	20 (23.3)	9 (39.1)	29 (26.6)
TOTAL	86	23	109

Table 2. Age class structures (%) of gopher tortoise populations from McRae et al. 1981 (n= 455), McLaughlin 1990 (n=111), Diemer 1992 (n=351), Rostal and Jones 2002 (n=175) and the present study (n=85). *percentages calculated exclude hatchling tortoises to allow for comparison.

	JUVENILE	SUB-ADULT	ADULT
McRae et al. 1981	9.1	9.1	81.2
McLaughlin, 1990	14.4	16.2	69.4
Diemer, 1992	34.8	17.7	47.6
Rostal and Jones, 2002	1.1	13.7	81.7
Present Study	45.3*	21.8*	32.9*

Table 3. A review of gopher tortoise egg, nest and hatchling characteristics from previous studies in comparison to the present study at WOP.

Mean egg diameter (mm)	Mean egg mass (g)	Mean Clutch Size (range)	Emergence dates (range)	Hatching success (%)	Hatchling CL (mm)	Location	Source
40.1	40.4	3.8 (2-7)	9/4-10/6	87.5	46.8	North Florida	Present study
43.5	n/a	6.5 (6-7)	9/4-9/25	92	43.4	Central Florida	Arata, 1958
42.2	37.7	5.04 (3-8)	8/18-10/5	80.6/82.3	n/a	North Florida	Butler and Hull, 1996
n/a	n/a	5.8 (3-10)	n/a	n/a	n/a	Central Florida	Diemer and Moore, 1994
n/a	n/a	4.8	8/16-9/22	28.8	48.3	Mississippi	Epperson and Heise, 2003
41.6	n/a	5 (4-7)	n/a	n/a	n/a	North Florida	Hallinan, 1923
43.3	40.9	5.2 (1-9)	8/20-9/29	n/a	n/a	North Florida	Iverson, 1980
44.8	44.5	7 (4-12)	8/29-10/9	86	n/a	Southwest Georgia	Landers et al., 1980
n/a	38.1	n/a	n/a	28	n/a	Florida	Linley and Mushinsky, 1994
n/a	n/a	6.9	8/8-9/21	n/a	49.7	Southwest Florida	McLaughlin, 1990
41.6	n/a	10.1 (8-13)	n/a	n/a	n/a	Southeast Florida	Moore et al., 2009
n/a	40.7/42.6	4.52/6.52 (3-12)	n/a	84.5	46.4	Southern Georgia	Rostal and Jones, 2002
n/a	n/a	n/a	8/24-10/2	67-97	n/a	Florida	Smith, 1995
43.3	39.4	3.8	n/a	n/a	n/a	South Carolina	Wright, 1982

APPENDIX

Raw Data: Burrows (GPS coordinates are in decimal degrees).

	2010 Occupancy	2011 Occupancy	Size	Site	Lat_DD	Long_DD	Transect
1	Active	Active	Juvenile	B	30.74978	-81.74632	-
2	Inactive	Inactive	Juvenile	B	30.74982	-81.74630	-
3	Active		Sub-Adult	B	30.74985	-81.74620	E border S
4	Active		Sub-Adult	B	30.75308	-81.74957	-
5	Active	Active	Adult	A	30.75345	-81.75338	D-E
6	Active	Abandoned	Adult	A	30.75357	-81.75330	D-E
7	Inactive		Juvenile	A	30.75358	-81.75287	-
8	Active		Juvenile	A	30.75367	-81.75255	F-G
9	Active	Active	Juvenile	A	30.75368	-81.75232	H-I
10	Active	Active	Adult	A	30.75373	-81.75227	H-I
11	Active	Active	Sub-Adult	A	30.75350	-81.75222	H-I
12	Active	Active	Sub-Adult	A	30.75337	-81.75315	E-F
13	Inactive	Abandoned	Juvenile	A	30.75360	-81.75295	E-F
14	Active		Sub-Adult	A	30.75367	-81.75303	E-F
15	Active	Abandoned	Sub-Adult	A	30.75360	-81.75305	E-F
16	Inactive	Active	Sub-Adult	A	30.75345	-81.75288	F-G
17	Inactive	Abandoned	Adult	A	30.75343	-81.75283	F-G
18	Active		Juvenile	A	30.75345	-81.75263	F-G
19	Active	Active	Juvenile	A	30.75370	-81.75247	G-H
20	Active	Active	Sub-Adult	A	30.75387	-81.75245	G-H
21	Abandoned		Sub-Adult	A	30.75370	-81.75248	G-H
22	Inactive	Abandoned	Sub-Adult	A	30.75380	-81.75235	H-I
23	Abandoned		Juvenile	A	30.75352	-81.75218	I-J
24	Inactive	Abandoned	Sub-Adult	A	30.75400	-81.75238	H-I
25	Active	Active	Juvenile	A	30.75400	-81.75242	H-I
26	Abandoned		Sub-Adult	A	30.75393	-81.75235	H-I
27	Active	Abandoned	Juvenile	A	30.75370	-81.75235	H-I
28	Active	Active	Adult	A	30.75377	-81.75205	I-J
29	Active		Juvenile	A	30.75343	-81.75183	J-K
30	Active	Active	Adult	A	30.75362	-81.75185	J-K
31	Active	Active	Adult	A	30.75402	-81.75192	J-K
32	Active	Inactive	Adult	A	30.75400	-81.75198	I-J
33	Active		Juvenile	A	30.75387	-81.75198	I-J
34	Active		Juvenile	A	30.75388	-81.75197	I-J
35	Active	Active	Adult	A	30.75365	-81.75190	I-J
36	Active	Active	Juvenile	A	30.75365	-81.75173	J-K
37	Active		Sub-Adult	A	30.75370	-81.75173	J-K
38	Inactive		Adult	A	30.75368	-81.75167	J-K
39	Active	Active	Sub-Adult	A	30.75372	-81.75168	J-K
40	Active		Adult	A	30.75362	-81.75183	J-K

41	Active		Adult	A	30.75355	-81.75168	J-K
42	Active		Juvenile	A	30.75342	-81.75153	J-K
43	Inactive		Juvenile	A	30.75363	-81.75153	K-L
44	Active		Adult	A	30.75370	-81.75153	K-L
45	Active		Sub-Adult	A	30.75363	-81.75148	K-L
46	Active	Active	Hatchling	A	30.75390	-81.75163	J-K
47	Abandoned	Active	Adult	A	30.75397	-81.75162	J-K
48	Active	Active	Adult	A	30.75430	-81.75158	K-L
49	Active	Abandoned	Adult	A	30.75402	-81.75177	J-K
50	Active	Active	Adult	A	30.75430	-81.75142	K-L
51	Abandoned		Sub-Adult	A	30.75418	-81.75158	K-L
52	Active	Inactive	Adult	A	30.75382	-81.75162	K-L
53	Active	Abandoned	Juvenile	A	30.75370	-81.75147	K-L
54	Inactive		Juvenile	A	30.75362	-81.75142	K-L
55	Active	Abandoned	Adult	A	30.75357	-81.75140	K-L
56	Inactive		Juvenile	A	30.75355	-81.75138	K-L
57	Inactive		Sub-Adult	A	30.75360	-81.75130	K-L
58	Inactive		Juvenile	A	30.75352	-81.75135	L border
59	Inactive		Juvenile	A	30.75383	-81.75145	K-L
60	Active		Juvenile	A	30.75390	-81.75143	K-L
61	Active		Juvenile	A	-	-	K-L
62	Active	Active	Adult	A	30.75403	-81.75145	K-L
63	Active	Active	Adult	A	30.75420	-81.75133	L-M
64	Active	Inactive	Juvenile	A	30.75422	-81.75142	K-L
65	Abandoned		Sub-Adult	A	30.75443	-81.75147	K-L
66	Abandoned		Sub-Adult	A	30.75443	-81.75147	K-L
67	-		-	A	-	-	-
68	Active	Active	Adult	A	30.75373	-81.75107	L-M
69	Active	Active	Juvenile	A	30.75395	-81.75107	M-N
70	Active	Active	Juvenile	A	30.75398	-81.75107	L-M
71	Active	Inactive	Adult	A	30.75417	-81.75125	L-M
72	Active	Active	Adult	A	30.75390	-81.75082	M-N
73	Inactive		Sub-Adult	A	30.75418	-81.75083	N border
74	Active		Adult	A	30.75428	-81.75082	N-O
75	Active	Active	Juvenile	A	30.75338	-81.75022	P-Q
76	Active	Active	Adult	A	30.75328	-81.74962	S-T
77	Active		Sub-Adult	A	30.75327	-81.74885	V-W
78	Active	Active	Adult	A	30.75347	-81.74818	Y-Z
79	Active	Active	Adult	A	30.75360	-81.74802	Y-Z
80	Active	Active	Adult	A	30.75370	-81.74790	Z-AA
81	Active	Active	Adult	A	30.75357	-81.74758	AA-BB
82	Active	Active	Adult	A	30.75378	-81.74772	Z-AA
83	Active	Inactive	Adult	A	30.75378	-81.74772	Z-AA
84	Inactive		Adult	A	30.75420	-81.74718	CC border
85	Active		Adult	A	30.75382	-81.74682	DD border
86	Abandoned		Adult	A	30.75402	-81.74707	CC-DD
87	Active		Adult	A	30.75383	-81.74653	EE-FF
88	Active		Sub-Adult	A	30.75415	-81.74647	EE-FF
89	Active		Adult	B	30.74777	-81.74400	Triangle
90	Active		Adult	B	30.74787	-81.74392	Triangle

91	Abandoned		Sub-Adult	A	30.75365	-81.75370	-
92	Active		Adult	A	30.75373	-81.75315	E-F
93	Active		Juvenile	A	30.75383	-81.75247	H-I
94	Active		Juvenile	A	30.75392	-81.75243	H-I
95	Active		Adult	A	30.75410	-81.75205	H-I
96	Active	Active	Juvenile	A	30.75388	-81.75097	M-N
97	Active	Active	Juvenile	A	30.75360	-81.75132	L-M
98	Active	Abandoned	Juvenile	A	30.75355	-81.75145	K-L
99	Active	Active	Juvenile	A	30.75355	-81.75145	K-L
100	Active	Active	Juvenile	A	30.75343	-81.75198	I-J
101	Active	Active	Juvenile	A	30.75347	-81.75202	I-J
102	Active	Active	Adult	A	30.75358	-81.75247	G-H
103	Active	Active	Sub-Adult	A	30.75357	-81.75260	G-H
104	Active	Active	Juvenile	A	30.75355	-81.75263	G border
105	Active	Active	Adult	A	30.75350	-81.75262	F-G
106	Active	Active	Sub-Adult	A	30.75338	-81.75303	E-F
107	Inactive		Sub-Adult	A	30.75340	-81.75322	D-E
108	Active	Abandoned	Adult	A	30.75345	-81.75332	D-E
109	Active		Juvenile	B	30.74932	-81.74533	B border S
110	Abandoned		Adult	B	30.74938	-81.74500	B-C south
111	Inactive		Sub-Adult	B	30.74938	-81.74505	B-C south
112	Active		Adult	B	30.74950	-81.74522	B-C south
113	Inactive		Juvenile	B	30.74953	-81.74523	B-C south
114	Inactive		Sub-Adult	B	30.74943	-81.74545	B-C south
115	Abandoned		Adult	B	30.74950	-81.74585	C border S
116	Active		Adult	B	30.74953	-81.74583	B-C south
117	Abandoned	Abandoned	Adult	B	30.74958	-81.74585	C-D south
118	Abandoned		Juvenile	B	30.74957	-81.74588	C-D south
119	Active	Active	Sub-Adult	B	30.74957	-81.74592	C-D south
120	Active		Sub-Adult	B	30.74973	-81.74597	D-E south
121	Active		Adult	B	30.74978	-81.74590	D-E south
122	Active	Inactive	Adult	B	30.74973	-81.74578	D border S
123	Active	Active	Adult	B	30.74968	-81.74503	C-D south
124	Active	Active	Juvenile	B	30.74978	-81.74512	D border S
125	Active	Active	Sub-Adult	B	30.74978	-81.74525	D-E south
126	Active		Sub-Adult	B	30.74990	-81.74527	D-E south
127	Inactive		Sub-Adult	B	30.74995	-81.74533	D-E south
128	Abandoned		Juvenile	B	30.74995	-81.74535	E-F south
129	Abandoned	Abandoned	Adult	B	30.74967	-81.74583	C-D south
130	Active	Abandoned	Juvenile	B	30.74965	-81.74578	C-D south
131	Abandoned		Adult	B	30.74982	-81.74593	D-E south
132	Abandoned	Abandoned	Adult	B	30.74983	-81.74593	D-E south
133	Active		Sub-Adult	B	30.74985	-81.74588	E border S
134	Active		Juvenile	B	30.74983	-81.74517	D-E south
135	Active	Active	Juvenile	B	30.74988	-81.74502	D-E south
136	Active	Active	Adult	B	30.74988	-81.74503	D-E south
137	Active	Active	Adult	B	30.75000	-81.74507	E-F south
138	Abandoned	Abandoned	Adult	B	30.74987	-81.74562	D-E south
139	Abandoned		Adult	B	30.74987	-81.74572	D-E south
140	Active		Juvenile	B	30.75063	-81.74592	-

141	Inactive		Adult	A	30.75360	-81.75278	-
142	Active		Juvenile	A	30.75357	-81.75185	J border
143	Inactive		Juvenile	A	30.75358	-81.75178	J-K
144	Active		Juvenile	A	30.75362	-81.75173	J-K
145	Active	Active	Juvenile	A	-	-	J-K
146	Active	Inactive	Juvenile	A	30.75345	-81.75100	M border
147	Active		Juvenile	A	30.75353	-81.74818	X-Y
148	Active		Adult	A	30.75392	-81.74660	EE-FF
149	Abandoned		Adult	A	30.75387	-81.74673	DD-EE
150	Active		Adult	A	30.75377	-81.74750	AA-BB
151	Abandoned		Adult	A	30.75330	-81.74960	S-T
152	-		-	-	-	-	-
153	-		-	-	-	-	-
154	-		-	-	-	-	-
155	Active	Active	Juvenile	B	30.74995	-81.74603	F-G south
156	Active	Active	Adult	B	30.74997	-81.74605	F-G south
157	Active	Active	Sub-Adult	B	30.75028	-81.74593	F-G south
158	Active	Active	Juvenile	B	30.75035	-81.73460	G-H south
159	Active	Active	Adult	B	30.75045	-81.74595	F-G south
160	Active	Active	Juvenile	B	30.75035	-81.74598	G south
161	-		-	-	-	-	-
162	-		-	-	-	-	-
163	-		-	-	-	-	-
164	-		-	-	-	-	-
165	-		-	-	-	-	-
166	Inactive		Juvenile	A	30.75325	-81.75372	C-D
167	Inactive		Juvenile	A	30.75365	-81.75307	E-F
168	Inactive		Sub-Adult	A	30.75352	-81.75272	F-G
169	Active		Juvenile	A	30.75343	-81.75262	G-H
170	Active		Juvenile	A	30.75347	-81.75260	G-H
171	Active		Juvenile	A	30.75385	-81.75243	H-I
172	Active		Hatchling	A	30.75357	-81.75245	H-I
173	Active		Juvenile	A	30.75365	-81.75240	H-I
174	-	-	-	-	-	-	-
175	-	Inactive	-	A	-	-	I-J
176	-	Inactive	-	A	-	-	I-J
177	-	Abandoned	-	A	-	-	I-J
178	Active		Adult	A	30.75385	-81.75205	I-J
179	Abandoned		Sub-Adult	A	30.75408	-81.75203	I-J
180	Active		Juvenile	A	30.75415	-81.75208	I-J
181	Active	Active	Juvenile	A	30.75343	-81.75168	J-K
182	Active		Juvenile	A	30.75342	-81.75175	J-K
183	Active	Active	Juvenile	A	30.75337	-81.75162	J-K
184	Active	Active	Juvenile	A	30.75353	-81.75153	K-L
185	Abandoned	Abandoned	Adult	A	30.75392	-81.75148	K-L
186	Inactive	Active	Juvenile	A	30.75393	-81.75155	K-L
187	Abandoned		Adult	A	30.75410	-81.75107	L-M
188	Active		Juvenile	A	30.75378	-81.75115	L-M
189	Active		Juvenile	A	30.75378	-81.75123	L-M
190	Active	Active	Sub-Adult	A	30.75353	-81.74747	AA-BB

191	Active		Sub-Adult	A	30.75398	-81.74712	BB-CC
192	Active		Sub-Adult	A	30.75350	-81.75098	M-N
193	Active		Juvenile	A	30.75352	-81.75095	M-N
194	Active		Sub-Adult	A	30.75363	-81.75097	M-N
195	Active		Hatchling	A	30.75380	-81.75097	M-N
196	Active	Active	Juvenile	A	30.75403	-81.75093	M-N
197	Active	Active	Sub-Adult	A	30.75368	-81.75080	N-O
198	Active		Juvenile	A	30.75402	-81.75070	N-O
199	Active		Juvenile	A	30.75385	-81.75123	L-M
200	Inactive		Juvenile	A	30.75350	-81.74787	Z-AA
201	Inactive		Juvenile	A	30.75377	-81.74708	CC-DD
202	Active		Juvenile	A	30.75365	-81.75155	J-K
203	Active	Active	Juvenile	A	30.75365	-81.75148	K-L
204	Active		Juvenile	A	30.75363	-81.75132	K-L
205	Active		Juvenile	A	30.75358	-81.74978	R-S
206	Abandoned	Active	Adult	A	30.75348	-81.74982	R-S
207	Abandoned		Adult	A	30.75368	-81.74930	T-U
208	Inactive		Adult	A	30.75395	-81.74900	V-W
209	Inactive		Sub-Adult	A	30.75422	-81.74683	CC-DD
210	Inactive		Adult	A	30.75323	-81.75327	D-E
211	Active		Juvenile	A	30.75353	-81.75192	
212	Active		Sub-Adult	A	30.75423	-81.75082	M-N
213	Active		Juvenile	A	30.75375	-81.75123	L-M
214	Active		Juvenile	A	30.75362	-81.75110	L-M
215	Active		Juvenile	A	30.75355	-81.75127	L-M
216	Active	Active	Sub-Adult	A	30.75372	-81.75198	I-J
217	Active	Active	Sub-Adult	B	30.74997	-81.74528	E-F south
218	Active	Active	Adult	B	30.75018	-81.74535	E-F south
219	Active	Active	Adult	B	30.75058	-81.74580	H-I south
220	Active		Adult	B	30.75068	-81.74567	H-I south
221	Active		Adult	B	30.74985	-81.74478	D-E south
222	Active		Juvenile	A	30.75390	-81.75235	H-I
223	Active	Active	Juvenile	A	30.75353	-81.75212	H-I
224	Active	Abandoned	Juvenile	A	30.75355	-81.75212	H-I
225	Active	Abandoned	Juvenile	A	30.75345	-81.75162	H-I
226	Active		Juvenile	A	30.75352	-81.75165	H-I
227	Active	Active	Juvenile	B	30.75037	-81.74605	H-I south
228	Active		Adult	B	30.75040	-81.74550	G-H south
229	Active	Active	Adult	B	30.74813	-81.74422	Triangle
230	Active	Active	Adult	A	30.75377	-81.75072	M-N
231	n/a	Active	Juvenile	A	30.75385	-81.75127	L-M
232	n/a	Active	Juvenile	A	30.75353	-81.75195	I-J
233	n/a	Active	Adult	B	30.76662	-81.74530	E-F south
234	n/a	Active	Hatchling	B	30.75012	-81.74530	E-F south
235	n/a	Active	Sub-Adult	B	30.75012	-81.74548	F-G south
236	n/a	Active	Adult	B	30.75008	-81.74517	E-F south
237	n/a	Active	Hatchling	B	30.75000	-81.74507	-
238	n/a	Active	Hatchling	B	30.74998	-81.74515	-
239	n/a	Active	Juvenile	A	30.75370	-81.75172	J-K
240	n/a	Active	Juvenile	A	30.75358	-81.75225	H-I

241	n/a	Active	Juvenile	A	30.75338	-81.75183	I-J
242	n/a	Active	Juvenile	A	30.75358	-81.75117	L-M
243	n/a	Active	Juvenile	A	30.75348	-81.74798	Y-Z
244	n/a	Active	Adult	A	30.75318	-81.75050	N-O
245	n/a	Active	Juvenile	A	30.75432	-81.75183	J-K
246	n/a	Inactive	Sub-Adult	A	30.75343	-81.75100	M-N
247	n/a	Abandoned	Adult	A	30.75392	-81.75208	I-J
248	n/a	Active	Juvenile	A	30.75403	-81.75150	K-L
249	n/a	Active	Sub-Adult	B	30.75023	-81.74530	-
250	n/a	Active	Sub-Adult	B	30.75050	-81.74587	-
251	n/a	Active	Adult	B	30.74968	-81.74570	C-D south
252	n/a	Active	Adult	B	30.74967	-81.74563	B-C south
253	n/a	Active	Adult	B	30.74968	-81.74547	-
254	n/a	Active	Adult	B	30.75012	-81.74550	E-F south
255	n/a	Active	Adult	B	30.75022	-81.74552	F-G south
256	n/a	Active	Adult	B	30.75042	-81.74597	-
257	n/a	Active	Hatchling	A	30.75367	-81.75228	H-I
258	n/a	Active	Hatchling	B	30.75022	-81.74550	E-F south
259	n/a	Active	Juvenile	A	30.75383	-81.75150	J-K
260	n/a	Active	Juvenile	B	30.74988	-81.74528	E-F south
261	n/a	Active	Juvenile	B	30.74950	-81.74480	B-C south
262	n/a	Active	Sub-Adult	B	30.74997	-81.74603	-
263	n/a	Active	Juvenile	A	30.75333	-81.75283	-
264	n/a	Active	Juvenile	A	30.75335	-81.75178	J-K
265	n/a	Active	Hatchling	A	30.75343	-81.75265	F-G
266	n/a	Active	Sub-Adult	B	30.75012	-81.74542	-
267	n/a	Active	Adult	A	30.75342	-81.74917	U-V
268	n/a	Active	Juvenile	B	30.74997	-81.74603	-
269	n/a	Active	Juvenile	A	30.75332	-81.75145	K-L
270	n/a	Active	Hatchling	A	30.75355	-81.75137	K
271	n/a	Active	Juvenile	A	30.75340	-81.75180	J-K
272	n/a	Active	Juvenile	A	30.75365	-81.75230	H-I
273	n/a	Active	Juvenile	A	-	-	L-M
274	n/a	Active	Juvenile	A	-	-	L-M
275	n/a	Active	Juvenile	A	30.75343	-81.75080	M-N
276	n/a	Active	Juvenile	A	30.75355	-81.75170	J-K
277	n/a	Active	Adult	A	30.75380	-81.74668	EE-FF
278	n/a	Active	Juvenile	A	30.75380	-81.75067	N-O
279	n/a	Active	Juvenile	A	30.75348	-81.75095	M-N
280	n/a	Active	Sub-Adult	A	30.75358	-81.75048	N-O
281	n/a	Active	Juvenile	A	-	-	N-O
282	n/a	Active	Juvenile	A	30.75380	-81.75045	N-O
283	n/a	Active	Juvenile	A	30.75373	-81.75047	N-O
284	n/a	Active	Juvenile	A	30.75363	-81.75082	M-N
285	n/a	Active	Juvenile	A	30.75367	-81.75075	N border
286	n/a	Active	Juvenile	A	30.75368	-81.75055	N-O
287	n/a	Active	Sub-Adult	A	30.75332	-81.74875	V-W
288	n/a	Active	Juvenile	A	30.75423	-81.75177	M-N
289	n/a	Active	Juvenile	A	30.75390	-81.75127	L-M
290	n/a	Active	Juvenile	B	30.74993	-81.74512	D-E south

291	n/a	Active	Juvenile	A	30.75347	-81.75092	N-O
292	n/a	Active	Sub-Adult	B	30.74995	-81.74538	D border S
293	n/a	Active	Hatchling	A	30.75382	-81.75230	H-I
294	n/a	Active	Adult	A	30.75317	-81.75357	C-D
295	n/a	Active	Juvenile	A	30.75395	-81.75092	M-N
296	n/a	Active	Juvenile	B	30.74997	-81.74572	D-E south
297	n/a	Active	Juvenile	A	30.75408	-81.75028	N border
298	n/a	Active	Juvenile	A	30.75393	-81.75075	N-O
299	n/a	Active	Hatchling	A	30.75345	-81.75212	I border
300	n/a	Active	Juvenile	A	30.75355	-81.75142	K-L
301	n/a	Active	Juvenile	A	30.75345	-81.75253	G-H
302	n/a	Active	Juvenile	A	30.75343	-81.75097	N border
303	n/a	Active	Hatchling	A	30.75375	-81.75170	J-K
304	n/a	Active	Hatchling	A	30.75403	-81.75185	J-K
305	n/a	Active	Juvenile	B	30.75025	-81.74530	E-F south
306	n/a	Active	Hatchling	A	30.75378	-81.75232	H-I
307	n/a	Active	Hatchling	A	30.75367	-81.75238	H border
308	n/a	Active	Sub-Adult	A	30.75330	-81.75265	F-G
309	n/a	Active	Juvenile	A	30.75385	-81.75138	L border
310	n/a	Active	Hatchling	A	30.75383	-81.75148	K-L
311	n/a	Active	Juvenile	A	30.75352	-81.75217	I border
312	n/a	Active	Hatchling	A	30.75372	-81.75230	H-I

Raw Data: Tortoises (CL = carapace length, CW = carapace width, PL = plastron length, SH = shell height, TL = total length).

	Age Class	Site	Associated Burrows	CL (cm)	CW (cm)	PL (cm)	SH (cm)	TL (cm)	Weight (g)
1	Juvenile	B	140	8.9	7.3	8.5	-	9.1	-
2	Juvenile	A	147	8	6.5	7.6	-	8.2	-
3	Male	A	68	26.6	20	26.6	11.9	28.2	4000
4	Juvenile	A	n/a	-	-	-	-	-	-
5	Juvenile	A	191	10.6	8	10.2	-	10.9	220
6	Juvenile	A	36	10.5	8.1	9.8	4.4	-	350
7	Male	A	n/a	28.7	22	28.7	12.5	-	-
8	Juvenile	A	33	10.9	8.6	10.5	4.6	-	360
9	Sub-Adult	A	9,103,170	14.2	10.9	14.1	6.2	-	680
10	Juvenile	A	101	9.45	7.75	9.1	4.25	9.65	160
11	Juvenile	A	47	8.2	6.5	7.7	4.1	8.4	280
12	Juvenile	A	203,289	10.5	8.5	9.75	5.1	-	220
13	Juvenile	A	97	8.9	7.25	8.8	4.25	-	145
14	Juvenile	A	46	10.7	8.3	10.5	5.4	11.1	380
15	Sub-Adult	A	31	20.2	15.3	19.6	9.5	22.3	1500
16	Hatchling	A	224	5.66	5.04	5.24	2.98	5.77	45
17	Male	A	62	23.5	19	22.7	11.4	26.5	2800
18	Male	B	136,137	26.5	20.6	26.4	11.5	27.5	4100
19	Sub-Adult	A	85	22.5	17.6	23	9.9	23.9	2700
20	Juvenile	B	n/a	10.67	8.55	10.6	4.7	11	260

21	Female	A	52	26.5	18.4	26.2	11.8	28.6	3600
22	Sub-Adult	A	64	12.8	9.8	12.6	5.5	13.3	400
23	Sub-Adult	A	11	15.2	11.6	14.8	6.7	15.5	900
24	Juvenile	A	25	10.3	8.1	10.1	4.7	10.4	190
25	Juvenile	A	211	9.9	8.1	9.9	4.7	10.27	205
26	Sub-Adult	A	85	22.4	18.1	23	9.8	24.3	2700
27	Male	B	n/a	27.4	19.4	27.1	11.4	29.1	3900
28	Sub-Adult	A	49	19.1	19.3	19.1	8.1	19.9	1500
29	Male	A	49	26.9	21.4	27.9	12.6	29.9	4600
30	Male	B	228	27.9	21.3	28.4	12.3	29.4	4400
31	Male	B	137	25.2	18.4	25.3	11	26.8	3400
32	Juvenile	B	227	9.25	7.42	8.95	4.23	9.5	150
33	Male	A	78	24.6	18.4	25.1	10.7	25.8	3000
34	Female	A	35	28.5	22.5	26.5	12	30.1	4750
35	Female	A	10	24.6	17.7	24	9.9	25.5	3000
36	Male	A	79	27	20	24	12	-	3700
37	Female	A	72	28.5	21.4	28.5	12	29.9	3500
38	Female	B	233	27.3	21.7	27.8	11.7	29	4300
39	Male	A	28	25	21	24.2	11.3	27.7	3300
40	Female	A	28	28.9	22.5	26.8	12.2	30.3	3200
41	Juvenile	A	104	11.1	8.6	10.4	5.1	11.4	200
42	Female	B	137	26.7	20.3	26.3	12.2	28	3800
43	Female	B	n/a	25.9	18	26.2	11.1	26.7	3400
44	Juvenile	A	n/a	9.76	7.88	9.22	4.22	9.78	170
45	Juvenile	A	245	10.07	8.83	10.64	5.28	11.11	290
46	Sub-Adult	B	135	13.55	10.84	13.45	5.95	13.88	500
47	Male	B	159	25.5	18.8	25.7	10.8	26.6	3200
48	Juvenile	B	237	8.7	68.8	8.45	4.01	8.79	120
49	Juvenile	B	234	8.5	7.2	8.2	4.1	9.1	150
50	Hatchling	B	258	6.11	4.89	5.86	2.89	6.12	40
51	Juvenile	A	184	9.22	7.44	8.66	3.89	9.34	140
52	Hatchling	A	n/a	5.44	4.78	5.22	3	5.55	30
53	Hatchling	A	n/a	5.24	4.66	5.12	2.88	5.33	25
54	Hatchling	A	n/a	5.54	4.56	5.23	2.88	5.57	30
55	Hatchling	A	n/a	4.45	4.41	4.45	2.34	4.88	25
56	Juvenile	B	238	7.65	6.26	7.28	3.68	7.83	80
57	Male	A	n/a	24.9	19	24.7	10.9	26.2	3400
58	Hatchling	A	n/a	5.4	4.7	5.1	2.85	5.5	30
59	Hatchling	A	n/a	5.4	4.63	5.25	2.8	5.7	30
60	Juvenile	A	232	8.81	7.15	8.64	3.86	9.11	140
61	Male	B	n/a	28.2	21.1	29.4	12	30.3	4200
62	Juvenile	A	n/a	7.21	5.75	6.74	3.3	7.24	60
63	Sub-Adult	B	266	15	11.1	15.1	6.3	15.4	850
64	Male	A	32	28.4	21.3	28.8		20.5	4700
65	Hatchling	A	n/a	5.55	4.68	5.28	3.04	5.62	25
66	Sub-Adult	A	n/a	19.9	15	20.1	8.4	21.1	1700
67	Sub-Adult	B	126	17	13.1	17	7.3	17.6	1250
68	Hatchling	A	268	5.15	4.43	4.91	2.72	5.39	25
69	Juvenile	A	185,183	9.3	7.51	9.14	4.37	9.57	170
70	Juvenile	A	172	7.65	6.96	6.7	3.29	7.14	60

71	Juvenile	B	261	10.71	8.23	10.56	4.74	11.2	230
72	Juvenile	A	269	8.82	6.92	8.28	3.64	8.99	120
73	Hatchling	A	n/a	5.84	4.89	5.44	2.95	5.85	30
74	Juvenile	A	264	7.25	6.02	6.73	3.55	7.26	60
75	Sub-Adult	B	235,158	15.14	10.8	14.36	6.25	15.32	900
76	Male	A	72	27	20.3	27.8	-	29.2	4000
77	Sub-Adult	A	9	15.8	12.2	15.5	7.1	16.3	1000
78	Hatchling	A	293	5.54	4.74	5.33	2.83	5.74	30
79	Juvenile	A	146	9.8	7.5	8.75	4.54	9.82	130
80	Female	A	41	27	20.3	26.1	11.8	27.6	3800
81	Juvenile	A	181	9.69	7.31	8.98	4.21	9.68	145
82	Juvenile	A	275	10.4	8.29	10.02	4.54	10.65	235
83	Juvenile	A	240	12.1	9.2	11.6	5.5	12.1	300
84	Sub-Adult	B	217	20.2	14.7	20.5	8.2	21.1	1700
85	Female	A	244	26.6	20.2	26.5	12	28	4200
86	Juvenile	A	298	9.71	7.63	9.05	4.37	9.76	180
87	Juvenile	A	272	7.36	6.33	6.7	3.75	7.39	80
88	Sub-Adult	A	19	14.7	11.1	14.1	6.4	14.6	600
89	Sub-Adult	A	75	15.7	12	14.8	6.8	15.8	900
90	Female	A	63,48	26.1	20	24.4	12	28.2	3500
91	Sub-Adult	B	165	13.7	10.3	13.3	5.9	14.1	500
92	Male	A	76	25.1	18.4	24.6	10.6	25.4	3200
93	Sub-Adult	A	35	21	15	20.4	9.1	21.7	1800
94	Juvenile	A	248	9.57	7.77	9.21	4.08	9.68	150
95	Juvenile	A	n/a	10.96	8.57	10.97	4.86	11.41	270
96	Juvenile	A	309	9.71	7.72	9.22	4.41	9.77	170
97	Juvenile	A	301	7.56	6.23	7.14	3.62	7.67	80
98	Hatchling	A	n/a	4.4	4.01	4.17	2.8	4.43	25
99	Hatchling	A	n/a	4.58	4.07	4.3	2.7	4.67	25
	Hatchling	A	55	4.45	3.9	4.45	2.65	4.65	25
	Hatchling	A	55	4.6	4	4.5	2.6	4.7	25
	Hatchling	A	52	4.63	4.42	4.53	2.77	4.78	30
	Hatchling	A	52	4.72	4.48	4.58	2.58	4.8	30
	Hatchling	A	52	4.72	4.32	4.64	2.72	4.8	30
	Hatchling	A	63	4.75	4.28	4.75	2.86	5.01	25
	Hatchling	A	52	4.79	4.83	4.63	2.79	4.91	30
	Hatchling	A	52	4.81	4.47	4.87	2.85	5.01	35
	Hatchling	A	52	4.82	4.51	4.76	3.06	4.92	35
	Hatchling	A	63	4.85	4.33	4.85	2.72	5.05	30

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VITA

Julia “Rachel” Smith was born . She received her Bachelor’s degree in Ecology and Evolutionary Biology at the University of Arizona in 2008, at which point she accepted an internship opportunity in the Sea Turtle Conservation and Research Program at Mote Marine Laboratory in Sarasota, Florida. Following completion of the internship, Rachel taught two sections of the Introductory Biology lab at Arizona State University in the spring of 2009. Rachel was then accepted to graduate school at the University of North Florida and spent the next three years pursuing her Master’s degree in Biology. During her time at UNF, Rachel had the opportunity to be a contributing author on the petition to list the gopher tortoise as a federally threatened species in the eastern portion of their range. She was also a graduate teaching assistant and taught both General Biology and Anatomy and Physiology labs for the UNF biology department. After her three incredible years at UNF, Rachel is now a Research Fellow in wildlife biology at Walt Disney World, conducting research on both sea turtles and gopher tortoises.